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Trophic promiscuity, intraguild predation and the problem of omnivores

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Introduction

Does anybody else miss the good old days of trophic levels? When predators, herbivores and plants knew their place and interacted in appropriate linear chains (Hairston *et al.*, 1960; Oksanen, 1981)? We released biological control agents under the optimistic assumption that they would attack their designated prey, more or less, and at least leave organisms at other trophic levels well alone. We built management programmes and mathematical models based on this assumption (Berryman, 1992). We lived in simpler times.

No longer. Omnivores, apparently, are everywhere, practicing their trophic promiscuity in complex and dynamic fashion (Rosenheim, 2007). Predators eat predators, herbivores and, incorrigibly, sometimes plants (Coll & Guershon, 2002). Food chains have become passé, replaced by reticulate webs that defy our simple notions of stability as well as all sense of propriety (Polis *et al.*, 1989; Holt & Polis, 1997). We are face to face with the uncomfortable reality that our agents of control often eat more broadly than we would like them to. We live in the days of the omnivores.

Ecologists who work in unmanaged systems have long been acquainted with the vexing issue of omnivory. Random food webs built on Lotka–Volterra predator–prey equations become less stable with omnivory (Pimm, 1982), unless the omnivorous compartments (or loops) within the webs are characterized by weak links (Neutel *et al.*, 2007) or nonlinearities (McCann & Hastings, 1997). In other words, omnivory should be either rare or weak for systems to persist. Yet omnivory is apparently ubiquitous (Denno & Fagan, 2003; Arim & Marquet, 2004) and, judging by a casual glance at the ants alone, the links are hardly trivial (Davidson *et al.*, 2003; Helms & Vinson, 2008; Ottonetti *et al.*, 2008).

For entomologists who work in managed systems, questions of omnivory are taking centre stage in research on agents of biological control. The compatibility of multiple control agents, interactions between native and introduced predators, damage to crops and the spread of crop pathogens are all influenced by the degree to which insects practice omnivory. We have always worried, to some degree, about nontarget effects of biological control agents, but concerns most often were for species at the same trophic level as the target of our control efforts (Simberloff & Stiling, 1996; Hawkins & Marino, 1997; Louda & Stiling, 2004; Stiling, 2004). More and more, we recognize that nontarget effects of biological control agents can emerge at multiple trophic levels (Rosenheim *et al.*, 1995; Rosenheim, 1998) with the potential to compromise control efforts and influence associated ecosystems. High rates of omnivory may be responsible in part for the spread of exotic invasive predators and the decline of their native counterparts (Snyder *et al.*, 2004b), with successful invaders being those species with adaptations to counter the ravages of omnivorous predators (Sato & Dixon, 2004).

I have been thinking about this recently, in part because of the loss of our friend, colleague, and champion of omnivory research, Robert F. (Bob) Denno, who died last year. Others are more qualified to describe the profound and lasting influence that Bob had on the field of entomology. One of his interests in recent years was the study of omnivory, and his group helped to stimulate cutting-edge research on omnivores in natural and managed systems. This paper is not a tribute to Bob's research. Rather, his passing prompted me to think about the advances in omnivore research made during the last 5 years or so (I cheat with reference to a few important papers of finer vintage), and I present some highlights here with particular reference to managed systems.

Omnivores and intraguild predation: definitions

Omnivores are organisms that feed on more than one trophic level (Pimm & Lawton, 1978). Omnivores therefore include

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'herbivores' that engage in cannibalism, 'predators' that suck plant juices or consume seeds or pollen and 'predators' that feed on other predators as well as herbivores (Coll & Guershon, 2002; Denno & Fagan, 2003). Most of us are familiar with ants as prototypical omnivores. Many ant species will consume animal tissue, plant exudates, phloem, seeds (or their elaiosomes) and honeydew produced by herbivorous insects (Carroll & Janzen, 1973). At least for some ant species, omnivory is not simply a response to low resource availability. For example, colonies of the invasive red imported fire ant *Solenopsis invicta* in the southern U.S.A. grow 50% larger in the presence of honeydew-producing insects than they do when provided with unlimited access to insect prey (Helms & Vinson, 2008). Given that honeydew is generally thought to be a lower-quality resource than animal tissue (Speight *et al.*, 2008), there must be something about resource diversity that is important to fire ants.

A subset of omnivores, known as intraguild predators (Polis *et al.*, 1989), feed on prey items and the prey of their prey (Fig. 1). As a result, intraguild (IG) predators both eat IG prey and compete with them for resources. Intraguild predation (IGP) appears to be astonishingly common in nature, with 58–87% of species engaged in IGP interactions in the 113 food webs analysed by Arim and Marquet (2004). This is a staggering proportion of species, and a clear challenge to the notion of discrete trophic levels. According to a wide variety of models of intraguild predation (IGP), coexistence (stability) is possible only when the IG prey is a stronger competitor than the IG predator for the shared resource and only at intermediate levels of resource productivity (Holt & Polis, 1997; Borer *et al.*, 2007). At low resource productivity, the IG predator is excluded, whereas, at high resource productivity, the IG prey is excluded. Given the apparent prevalence of IGP in nature over wide ranges of resource productivity, there must be additional coexistence mechanisms that act to stabilize IGP interactions. These might include cannibalism among pre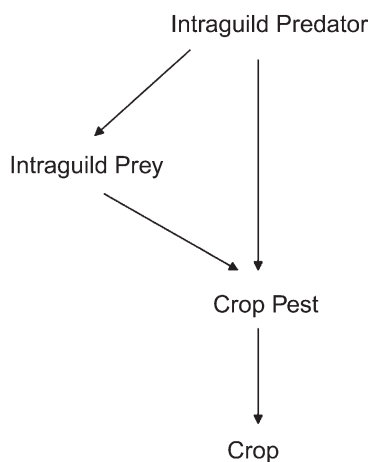dators (Rudolf, 2007), spatial or temporal refuges for the participants (Amarasekare, 2007; Janssen *et al.*, 2007), additional density-dependent processes operating on species (Ives *et al.*, 2005) or additional prey available to the consumers (Briggs & Borer, 2005; Holt & Huxel, 2007).

If all of the above sounds a bit abstract, consider an example. The harlequin bug *Murgantia histrionica* is a specialist herbivore on bladderpod *Isomeris arborea* in California. The eggs of the harlequin bug are parasitized by two specialist parasitoids, *Trissolcus murgantiae* and *Ooencyrtus johnsonii* (Amarasekare, 2000). Because they overlap in resource use (harlequin bug eggs) and because *O. johnsonii* consumes *T. murgantiae* (but not vice versa) when they co-occur, the system is an example of IGP; *O. johnsonii* is the IG predator and *T. murgantiae* is the IG prey. All species coexist over a broad range of resource productivity (i.e. new bug eggs per unit time) and, in this case, the interaction is apparently stabilized by a temporal refuge for the IG prey. *Trissolcus murgantiae* is active at cooler temperatures and has an early-season time window during which it is free from competition with, and predation by, *O. johnsonii* (Amarasekare, 2007).

I mentioned earlier that omnivory is apparently much more common than we once thought. Why should omnivory be common in nature? Omnivores are an interesting form of dietary generalists, extending their dietary breadth beyond their own trophic level to encompass prey items at additional trophic levels. A generalist diet is considered by some to evolve in response to a trade-off between dietary quality and dietary quantity, and this same logic has been applied to the evolution of insect omnivores (Denno & Fagan, 2003). For example, if the highest-quality food source for an organism is also the most abundant, there should be no selection pressure (or ecological benefit) for a generalist diet and specialization should result (Krebs & Davies, 1993). As described in some ancient religious texts, there are no omnivores in a world awash in manna. However, as the highest-quality food source becomes increasingly diluted by more common, lower quality food, dietary breadth should increase.

Denno and Fagan (2003) have suggested that omnivorous predators are supplementing their diet of low-nitrogen herbivores with higher-nitrogen predators. Omnivory, then, is seen as a strategy by which herbivore-eaters improve their lot. A complementary view might be that higher-order predators are required to incorporate lower quality herbivores into their diet because other predators are too rare as sources of food. In other words, the relative scarcity of prey with high concentrations of nitrogen in their body tissues (i.e. other arthropod predators) should result in the incorporation of herbivores (intermediate nitrogen concentrations) and plants (low nitrogen concentrations) into the diet of some predators. Omnivory is therefore favoured by the relative scarcity of food items that are good stoichiometric matches to the consumer. Of course, the evolution of omnivory is not just about stoichiometry (Matsumura *et al.*, 2004). Diet mixing in general can dilute toxins in food, reduce the risk of predation or parasitism, and increase resistance to natural enemies (Singer & Bernays, 2003). There are evolutionary challenges to omnivory because omnivores must be able to catch, handle, digest and assimilate a broader

Figure 1 A simple illustration of intraguild predation where the intraguild predator consumes the intraguild prey when competing with it for the crop pest. Pest suppression can be compromised, thus reducing crop yields.

range of prey types than their trophically-conservative relatives. We might therefore expect to see phylogenetic patterns in the evolution of omnivory and, indeed, we do. For example, within ancestrally herbivorous and ancestrally predaceous lineages of terrestrial heteropterans, seed and pollen feeding and broad host ranges are both correlated with the evolution of omnivory (Eubanks *et al.*, 2003). In other words, existing morphological and physiological traits can pre-adapt certain groups to an omnivorous lifestyle (Coll & Guershon, 2002).

Intraguild predation and the suppression of pests

Our efforts at biological control are often conceived under the assumption of simple food chains. They reflect our desire to manage trophic cascades (Paine, 1980; Carpenter *et al.*, 1985), whereby the abundance of top predators (agents of control) determines the standing crop of primary producers (our crops of interest) (Hunter & Price, 1992; Hunter, 2001). Omnivory may dampen the effects of trophic cascades (Strong, 1992; McCann *et al.*, 1998; Denno, 2007), reducing herbivore suppression by natural enemies and increasing plant damage (Finke & Denno, 2004, 2005). For those of us engaged in the control and management of insect pests, one question is obviously central: does the presence or introduction of multiple enemy species, including omnivores, increase or decrease pest suppression? In other words, how badly do intraguild predation and omnivory interfere with biological control? Quite often, the introduction of multiple agents of control results in the establishment of only a single dominant control agent (Denoth *et al.*, 2002). However, when multiple control agents are naturally or artificially established, what are the consequences for pest suppression?

First, consider simple models of IGP. We established above that IG predators and IG prey can sometimes coexist, through a variety of ecological mechanisms either intrinsic or extrinsic to their interactions. What does ecological theory tell us about the suppression of their shared prey: the pests of our production systems? As a reminder, we have to be careful to distinguish between pest 'production', which broadly describes the addition (birth, immigration) of new pest individuals per unit time, and the standing biomass of pests, which describes their average densities in the cropping system. Pest densities can be low, even if pest production is high, when rates of predation are also high.

With that in mind, theory predicts that the IG predator should become relatively more abundant (and the IG prey relatively less abundant) as pest productivity increases (Holt & Polis, 1997). Moreover, pest density should also increase as the IG predator increases in dominance. This is exactly what occurs in the dynamics of the iconic California red scale, *Aonidiella aurantii*, which is parasitized by *Aphytis melanus* (IG predator) and *Encarsia perniciosi* (IG prey). As the productivity (i.e. fecundity) of red scale increases among sites, there is an increase in the relative density of the IG predator, *A. melanus*, and a corresponding increase in scale

standing stock (density) (Borer *et al.*, 2003). What that means for pest managers, of course, is a higher pest density as the IG predator comes to dominate the dynamics. Simply put, simple theory tells us that IGP should reduce the suppression of pests by biological control agents.

However, empirical studies provide a greater range of outcomes than predicted by simple theory, and the literature includes examples of negative, neutral and positive interactions among predators that share prey resources. A recent meta-analysis has suggested that prey suppression is more often higher in diverse than in simple predator communities (Cardinale *et al.*, 2006), although issues of omnivory were not examined directly. In a second meta-analysis focused more specifically on omnivory, mutual IGP (when predator species can consume each other) was shown to compromise pest suppression in multi-predator systems, whereas unidirectional IGP (or the absence of IGP) did not (Vance-Chalcraft *et al.*, 2007). In other words, the strength and form of IGP in diverse predator communities appears to determine subsequent effects on pest suppression. As a gentle reminder, meta-analyses are usually aggregates of studies that report both significant positive and negative effects; the negative reports do not cease to be valid in their own right just because they are less common on average than the positive ones. Perhaps the more interesting question is why the effects of multi-predator species on pest suppression appear to be context dependent (Straub & Snyder, 2008).

We are making major progress in answering this question, in part because theory on interactions among predator species is being linked to theory on relationships between biodiversity and ecosystem processes (Ives *et al.*, 2005). We have learnt from these efforts that there exist at least four mechanisms by which predator diversity influences pest suppression. These are: (i) sampling (or lottery) effects (the presence or absence of dominant predators); (ii) resource partitioning among predators; (iii) indirect effects caused by intraguild predation; and (iv) non-additive effects among predators (Ives *et al.*, 2005). This is a critical observation because it allows us to reconcile studies in which increasing predator diversity is associated with either higher or lower levels of pest suppression. The relative importance of the four mechanisms described above in a particular production system of interest will probably determine whether high predator diversity increases or decreases crop yield. For example, we might expect that multiple predators with strong additive or synergistic effects will increase pest suppression and increase crop yields, whereas multiple predators engaged in high levels of intraguild predation should decrease pest suppression and crop yield (Rosenheim, 1998; Sih *et al.*, 1998; Snyder & Ives, 2003).

The study by Ives *et al.* (2005) provides a roadmap for future research on the effects of multi-predator species on pest suppression because a series of predictions is made that should be testable in production systems. For example, their analyses suggest that the sampling effect will tend to cause a reduction in pest densities as predator diversity increases, so long as predators vary in their assimilation efficiencies or capture rates. Likewise, resource partitioning by predators among multiple species of prey will also tend to cause reductions

in the average pest burden on plants as predator density increases. The latter effect of resource partitioning raises an important point: the predicted effects of predator–predator interactions on pest suppression depend upon the number of pest species within the production system. For example, if there is only one pest in the cropping system, or one that is dramatically more important to yield than all others, then IGP will probably lead to higher levels of crop damage. However, models also show that, in speciose pest communities, the total density of the entire herbivore community should still decline with increasing predator diversity when IGP is operating (Ives *et al.*, 2005). This suggests that crops with diverse pest species may suffer less overall damage with diverse predator populations, even when those predators engage in IGP. In brief, the overall impact of IGP on pest suppression depends in part on the diversity of pests in the cropping system. It appears that any negative impacts of IGP on pest suppression may be weak in comparison to the positive effects of predator diversity in multipest systems.

The apparent ubiquity of omnivory and intraguild predation (Arim & Marquet, 2004) has prompted much recent empirical work, aimed at untangling the effects of predator–predator interactions on herbivore suppression. In a series of clever experiments, Finke and Denno (2005) measured independently the effects of predator diversity and intraguild predation on herbivores and plants in a salt marsh ecosystem. They demonstrated that increasing predator diversity had little impact on herbivores and plants unless the predators engaged in intraguild predation. Under those circumstances, herbivore suppression declined and plant biomass was concomitantly reduced. Generalizing, multi-predator species appeared to be detrimental to plants when they engaged in intraguild predation.

Yet some notorious IG predators can apparently participate in successful biological control. In experimental studies of pea aphids *Acyrthosiphon pisum* on alfalfa in the Midwestern U.S.A., suppression of pea aphids is higher (with corresponding higher alfalfa yields) with higher diversity of natural enemies (Cardinale *et al.*, 2003). In this interesting case, the presence of generalist predators (*Harmonia axyridis* and *Nabis* sp.) causes declines in the associated cowpea aphid *Aphis craccivora* with the result that a key parasitoid, *Aphidius ervi*, focuses its prodigious powers of parasitism on pea aphids. The result is greater (non-additive) suppression of pea aphids than would be predicted from the sum of the effects of each enemy in isolation. Pest suppression occurs despite the fact that both *Harmonia* and *Nabis* are well-known omnivores, attacking other predators as well as herbivores (Snyder & Ives, 2003). What I particularly like about this study is that it includes measurements of crop yield, providing compelling evidence that growers should benefit from the presence of a diverse predator community. It also illustrates that positive indirect effects of high predator diversity can overcome simultaneous negative effects of IGP, as suggested by Ives *et al.* (2005).

Similarly, a diverse predator assemblage can result in suppression of aphid pests, and higher crop yields, in collards *Brassica oleracea* (Snyder *et al.*, 2006). In the U.S.A., collards are attacked by the green peach aphid *Myzus persicae*

and the cabbage aphid *Brevicoryne brassicae*. In turn, these aphids are attacked by a diverse predator assemblage, including the predatory bugs *Geocoris pallens* and *Nabis* spp., the ladybird beetles *Coccinella septempunctata* and *Hippodamia convergens*, and the parasitoid wasp *Diaeretiella rapae*. All of these predators are actually omnivores, engaging in IGP. As a result, IGP has the potential to interfere with pest suppression and increase levels of crop damage. Nonetheless, any negative effects of IGP on pest suppression are swamped by positive effects of predator complementarity, which keep aphid numbers low and increase collard production (Snyder *et al.*, 2006). Similar results were recently reported for potato (Straub & Snyder, 2008).

Glasshouse production systems may also benefit from multi-predator introductions, even in the presence of IGP. In the U.S.A., the aphid *Macrosiphum euphorbiae* is a significant pest of greenhouse-grown roses. It is attacked by the parasitoid *Aphelinus asychis*, which can also establish in greenhouses. It appears that simultaneous introduction of the parasitoid and the coccinellid beetle *H. axyridis* has no deleterious impact on aphid suppression by the parasitoid (Snyder *et al.*, 2004a). Rather, control is complementary, despite the fact that the beetle consumes mummified aphids that contain parasitoid pupae (intraguild predation). Biological control is improved in the presence of the beetle because it prefers to consume unparasitized, rather than parasitized, aphids.

What actions can pest managers take to reduce the probability that IGP will interfere with pest suppression under multi-predator biological control? One possibility might be to increase the heterogeneity of the cropping system. Evidence is accumulating that high habitat heterogeneity can ameliorate the negative effects of IGP on prey suppression. Structured habitats appear to provide refuges for IG prey from their IG predators, favouring the coexistence of multiple predator species (Finke & Denno, 2006; Janssen *et al.*, 2007). For example, in salt marsh ecosystems, spiders and mirid bugs combine to attack populations of *Prokelisia* planthoppers on *Spartina*. In the presence of abundant leaf litter (thatch), predators have refuges from IGP, with the result that plant hopper populations decline and plant biomass increases (Finke & Denno, 2006). In the absence of thatch, IGP prevents the trophic cascade from operating, and planthoppers cause declines in plant biomass. In the same system, habitat heterogeneity can also act to reduce rates of cannibalism among predators, a particularly unpleasant yet widespread form of intraguild predation (Langellotto & Denno, 2006). Although habitat heterogeneity does not always result in short-term pest suppression, (Langellotto & Denno, 2004; Janssen *et al.*, 2007)), long-term persistence of a diverse enemy pool may facilitate long-term suppression of pest populations as environments vary over time.

When predators eat plants

A tentative conclusion from the discussion above might be that omnivorous predators can still promote pest suppression and higher crop yields, at least in systems with multiple pest species and high habitat heterogeneity. However, what if

those predators also eat plants? Is there a place for crop-eating predators in biological control? Of course, there is a long evolutionary history of mutualism between plants and predators by which plants provide food or shelter for predators in return for predation services (Speight *et al.*, 2008). We might therefore expect that the benefits to plants of supporting plant-feeding predators should often outweigh the costs.

It turns out that many predators and parasitoids will consume plant material and still contribute to pest suppression. Zoophytophagy, the habit of consuming plant and animal tissue, is common in agroecosystems among the Heteroptera, Neuroptera, Thysanoptera, Phytoseiidae (Acarina) and Coccinellidae (Coleoptera) (Robinson *et al.*, 2008). Zoophytophagy can be beneficial to biological control, despite plant damage, if it maintains predator populations during periods of low prey abundance (Coll & Guershon, 2002). However, if the crop plants are chemically treated or genetically transformed, plant-feeding has the potential to reduce predator populations (Moser *et al.*, 2008).

Zoophytophagous bugs in the family Heteroptera are notorious omnivores, feeding on both plant tissue and insect prey. Indeed, the availability of suitable plant species for oviposition and feeding may increase Heteropteran performance and their subsequent efficacy as agents of control (Lundgren *et al.*, 2008). Typically, however, plants are assumed to be low-quality resources for zoophytophages, exploited largely when animal prey is at low abundance. For example, *Nesidiocoris tenuis* (Heteroptera: Miridae) is a zoophytophage on whitefly and tomatoes in greenhouse production systems. The occurrence of plant feeding by *N. tenuis* increases as its own density increases and decreases as whitefly prey become more abundant (Sanchez, 2008). Rapid decreases in *N. tenuis* populations after whitefly declines demonstrate that plants are poorer nutrient sources for predators than are whitefly prey. The benefits to omnivorous predators of plant-feeding may vary from simple water uptake in some systems to significant nutrient and energy gain in others (Robinson *et al.*, 2008; Sanchez, 2008). For example, the coccinellid beetle *Coleomegilla maculata* is an important biological control agent of corn pests in the U.S.A. It feeds on corn pollen during larval and adult stages, with adult pollen consumption exceeding a prodigious 13 mg per beetle (Lundgren *et al.*, 2005). Given such high potential consumption of plant resources by omnivores (Wackers *et al.*, 2008), it should be no surprise that there are commercially available 'nutrient supplements' for use with biological control agents. However, it is important to note that their value in pest suppression is not well established (Wade *et al.*, 2008).

Whether there is a net positive or negative effect of zoophytophagy on pest suppression may depend upon environmental conditions, including pest density and the period over which pest dynamics are measured. For example, adult lacewings consume floral resources (nectar, pollen) as well as aphid prey on buckwheat in New Zealand (Robinson *et al.*, 2008). In the presence of buckwheat flowers, lacewings consume fewer aphids each day, with an apparently negative effect of omnivory on pest suppression. However, at lower aphid densities, a propensity for flower-feeding reduces the pre-oviposition period of lacewing adults,

increasing their oviposition rates (i.e. a long-term positive effect on pest suppression at the population level). This is a key point: short-term experiments tend to illustrate potential negative impacts of omnivory and IGP on pest suppression that may be more than compensated for by long-term benefits under field conditions (Ives *et al.*, 2005; Robinson *et al.*, 2008).

As a final thought on zoophytophagy, plants engineered to express toxins might be expected to have negative impacts upon omnivorous predators, and such effects have been documented over the years subsequent to the deployment of transgenic plants. However, most effects appear to be weak. For example, the coccinellid *C. maculata*, and the invasive coccinellid *Harmonia axyridis* will feed on corn leaf tissue, even when aphid prey and water are in abundant supply (Moser *et al.*, 2008). Given that most corn in the U.S.A. is now transformed to express Bt toxins, coccinellids might suffer from feeding on transgenic corn. Rates of larval development in *C. maculata* appear to decline slightly when fed on Bt corn seedlings, but the effect is not particularly strong (Moser *et al.*, 2008).

Conclusions

With some exceptions, then, omnivores still appear to be our friends. They add diversity to the predator pool that is available to suppress the pests of our production systems. Their pathways of consumption may be reticulate and their interactions indirect, but they can often contribute to biological control in important ways. To maximize the benefits and minimize the risks associated with using omnivores in biological control, there are several lines of future work that would be beneficial. I have already mentioned the important predictions provided by the theoretical work of Ives *et al.* (2005) that need to be tested. Additionally, stable isotope analyses are providing more detailed descriptions of the relative consumption by omnivores of different food sources. For example, in Tuscan olive orchards, ^{13}C signatures demonstrate that ants gain energy from both olive-based and herb-based food webs. In the same system, different ant species vary in their use of plant-based and animal-based resources, as illustrated by their ^{15}N signatures (Ottonetti *et al.*, 2008). Such studies provide vital information on the energy pathways used by omnivores in production systems and appear to support the important role of habitat heterogeneity in mediating the positive impacts of omnivores in pest suppression. Moreover, as Bob Denno would have pointed out, we need to consider in much more detail how the behaviours and life histories of predators and prey influence the strength and direction of interactions in omnivorous food webs (Denno *et al.*, 2003; Rosenheim & Corbett, 2003; Singer & Bernays, 2003). We should also continue to explore effects of omnivory on pest suppression that appear influenced by ecological contingency, particularly variation caused by seasonality, habitat structure and nutrient availability (Gratton & Denno, 2003; Denno *et al.*, 2005). Omnivores may complicate our traditional naïve views of pest management, but there is no denying that they make life more interesting.

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